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Characterizing primate home-ranges in Amazonia: Using ferns and lycophytes as indicators of site quality

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Abstract

The habitats present in research sites across Amazonia have usually been characterized only very broadly, for example, as inundated or non-inundated (terra firma) forests. However, within each of these categories there is considerable variation in soil properties and floristic composition. This variation is likely to determine habitat quality for animal populations through its effects on primary productivity and food availability, thereby affecting carrying capacity. Therefore, comparison of edaphic properties across sites could provide new insight into which factors affect animal foraging patterns, population densities, and home-range sizes. We provide an example from Estación Biológica Quebrada Blanco in Peruvian Amazonia, where behavioral studies on primates (especially tamarins) have been conducted for more than three decades but little is known about the edaphic or floristic characteristics of the forest they occupy. We used indicator plant species to estimate and map soil base cation concentration and its variability at Estación Biológica Quebrada Blanco. We found that soils in the study area are relatively cation-poor in a western Amazonian context, which probably translates into low primary productivity. Some differences in soils among the home-ranges of three tamarin groups were also observed, illustrating the usefulness of the method for detailed habitat mapping.

Abstract in Spanish is available with online material.

KEYWORDS

ecological indicators, Estación Biológica Quebrada Blanco, habitat mapping, home-range, *Leontocebus nigrifrons*, Peru, primates, saddle-back tamarin

1 | INTRODUCTION

The habitats present in research sites across Amazonia have been only superficially characterized, using broad categories such as seasonally inundated and non-inundated (terra firma) forests. Within each of these categories, there is great variation in soil properties

and floristic composition, but these habitat differences are rarely reported. Edaphic characteristics, such as soil nutrient concentration and texture, have been shown to significantly affect the distributions of many plant groups, such as ferns and lycophytes ("pteridophytes"), palms (Arecaceae), and some shrub and tree families like Melastomataceae and Burseraceae (Cárdenas et al., 2007; Fine et al.,

Eckhard W. Heymann and Hanna Tuomisto share senior authorship.

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2005; Rodríguez et al., 2003; Ruokolainen et al., 2007; Salovaara et al., 2004; Suominen et al., 2013; Tuomisto, Poulsen, et al., 2003; Tuomisto, Ruokolainen, Aguilar, et al., 2003; Tuomisto, Ruokolainen, Yli-Halla, 2003; Tuomisto & Ruokolainen, 2005; Vásquez & Phillips, 2000; Vormisto et al., 2004).

Through its impact on plants, edaphic variation can be expected to determine habitat quality for animals. On nutrient-rich soils, plants typically grow faster than on nutrient-poor soils, resulting in higher primary productivity and greater resource allocation to fruit and flowers (Aragão et al., 2009; Chave et al., 2010; Malhi et al., 2014). Food quality may also be higher in rich-soil environments, since when nutrients are scarce, plants may invest more in chemical and structural defenses against herbivory (Fine et al., 2013). Both food quantity and quality can significantly limit the carrying capacity of the forest (Janzen, 1974; Kricher, 2011). For example, the production of fleshy fruits has been found to be positively related to the biomass of Neotropical primate assemblages (Stevenson, 2016). Differences in soil properties across sites can be used as an indicator of their relative productivity, and such knowledge can shed new light on why these sites vary in animal foraging patterns, population densities, and range sizes.

There is already evidence that different forest habitats in Amazonia harbor distinct animal species, and that habitat characteristics affect their distributions and abundances. For example, bird communities studied at sites located 4–400 km apart in Loreto, Peru, differed in their species composition, richness, and uniqueness among different soil and habitat types (Álvarez et al., 2013; Pomara et al., 2012). Studies in lowland Amazonia and the Guiana shield have found the biomass and population density of primates and other mammals to increase with increasing soil fertility (Palacios & Peres, 2005; Peres, 2008; Peres & Dolman, 2000). In some studies, these differences have been explicitly linked to geological formations (Salovaara et al., 2005). However, the degree to which bottom-up effects, especially resource availability (soil nutrients for plants, primary productivity for animals), impact primate behavior at the local scale has rarely been addressed even at otherwise well-studied sites.

The ecology and behavior of several primate species have been intensively studied at the Estación Biológica Quebrada Blanco (EBQB) in Peruvian Amazonia since 1984. Many of the studies have focused on tamarins, small (250–600 g) primates belonging to the genera *Saguinus* Hoffmannsegg and *Leontocebus* Wagner (Rylands et al., 2016). These are mainly frugivorous–insectivorous (Garber, 1993a; Rylands & Mittermeier, 2013) and typically live in groups of 3–10 individuals (Digby et al., 2007). Where two tamarin species from different genera occur in sympatry, they form stable mixed-species associations (Heymann & Buchanan-Smith, 2000).

Studies at EBQB have already revealed many different aspects of the ecology of saddle-back tamarins (*Leontocebus nigrifrons* L. Geoffroy Saint-Hilaire). These include their interactions with the mustached tamarin (*Saguinus mystax* Spix) and with birds (Heymann, 1992; Siegel et al., 1989). Their anti-predator behavior has also been investigated (Bartecki & Heymann, 1987; Lledo-Ferrer et al., 2009),

as has their role as seed dispersers (Culot et al., 2009; Heymann et al., 2019; Knogge et al., 1998, 2003; Knogge & Heymann, 2003; Tirado et al., 2003). Other studies have investigated their territorial behavior (Bartecki & Heymann, 1990; Heymann, 2001; Lledo-Ferrer et al., 2010, 2011), sleeping habits (Heymann, 1995; Smith et al., 2007), and feeding habits and strategies (Garber, 1988, 1993b; Nadjafzadeh & Heymann, 2008; Smith, 1999).

Despite the wealth of detailed studies on the ecology of saddle-back tamarins at EBQB, little is known about the forest they inhabit. A single study on foraging success in old-growth and secondary parts of the forest found that the capture rates of arthropod prey were lower in secondary forest (Kupsch et al., 2014). Whether there is local variation in more permanent habitat characteristics (e.g., soil nutrient concentration or drainage) that could be important for tamarin survival or behavior is not known. How the primary productivity or plant species composition at this site compares with other sites in Amazonia is likewise unknown. This makes it difficult both to take into account the possible effects of spatially variable resources when interpreting observed tamarin behavior, and to compare the results from EBQB with those from other sites in Amazonia. As a result, if differences in tamarin behavior are observed between EBQB and other sites, it is currently impossible to deduce whether these arise as a consequence of differences in habitat or due to other factors, such as interactions with other primates or spatial variation in intrinsic characteristics of the tamarins themselves.

Numerous studies have demonstrated that species composition of ferns and lycophytes can be used to predict soil properties in Amazonian forests (Tuomisto, Poulsen, et al., 2003; Tuomisto, Ruokolainen, Aguilar, et al., 2003; Tuomisto, Ruokolainen, Yli-Halla, 2003; Zuquim et al., 2014). Predictions of soil nutrient status, in turn, can be used to rank sites in terms of their expected primary productivity and food availability for forest animals (Sirén et al., 2013; Tuomisto et al., 2019). Therefore, fern and lycophyte inventories provide a relatively rapid approach to habitat characterization, and linking them to animal data makes it possible to test hypotheses concerning bottom-up control of animal population structure, dynamics, and behavior.

Here, we demonstrate the utility of this habitat mapping approach at EBQB in three ways. Specifically, our aims were to: (a) place the study area into the broader context of soil heterogeneity across Amazonian terra firma forests, (b) quantify and map within-site soil variation, and (c) combine inferred edaphic data with existing data on tamarin home-range sizes, to facilitate their ecological interpretation and future comparisons with other sites.

2 | METHODS

2.1 | Study area

We conducted field studies at the biological field station known as Estación Biológica Quebrada Blanco (EBQB), which is located about 90 km south of the city of Iquitos in northeastern Peru (4°21'S,

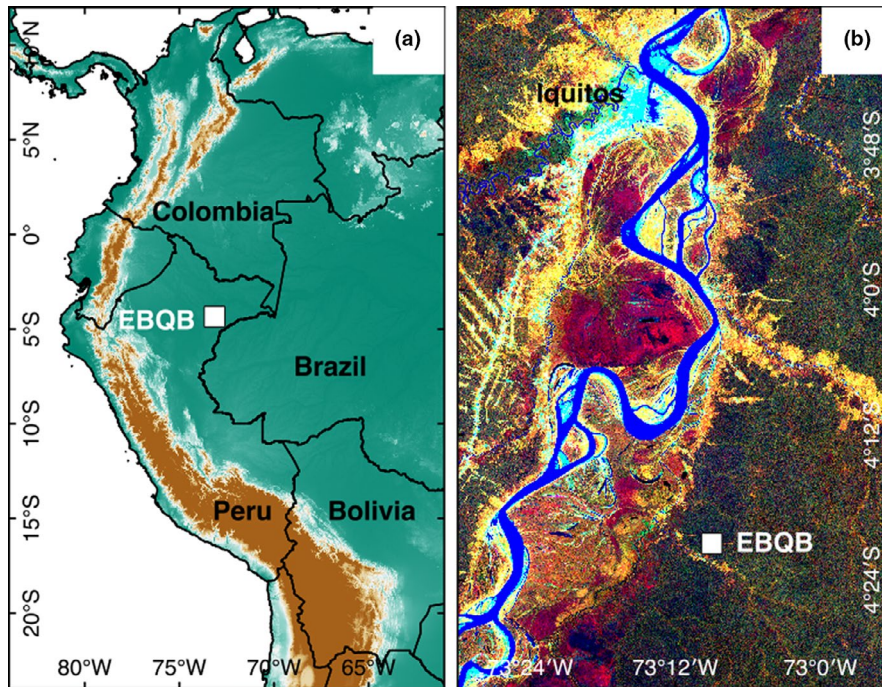


FIGURE 1 Location of the Estación Biológica Quebrada Blanco (EBQB; white square) in northern Peru. (a) Background map is based on the SRTM (Shuttle Radar Topography Mission) elevation model. (b) Background image is the Landsat TM/ETM+ composite of Van doninck and Tuomisto (2018)

73°09'W; Figure 1). The climate at EBQB is tropical and humid, with mean annual precipitation being 2400–3100 mm (Marengo, 1998). The terrain of the area is mostly flat, but strongly undulating areas occur in the central and western parts. The altitude is 110–150 m above sea level. According to satellite image interpretation (Kalliola et al., 1998), EBQB is located on an old terrace of the Amazon River. Most of the terrain is non-inundated (terra firma), but seasonally or occasionally inundated areas occur in the south-west and north-west corners, and waterlogged areas are found in the center (Heymann, 1995). EBQB is mostly in primary forest, but a small area of secondary forest (a former buffalo pasture that has been regenerating since 2000) exists in the south-eastern part of the study area (Heymann et al., 2019). EBQB has a trail system covering an area of 117 ha in the form of a rectangular grid with 100-m trail spacing. These trails were set up in 1984 by cutting 1–2 m wide swathes of understory vegetation (Heymann et al., 2014). The trails are marked every 100 m with labels referring to their west-east/north-south position.

2.2 | Tamarin studies

Three groups of saddle-back tamarin monkeys (referred to as G1, G2 and G3) habituated to human presence were tracked during 2004, 2007, and 2008. G1 and G3 were also tracked during 2009 and 2011. Although there are data available from earlier years, we did not include them in this study because they were collected without the use of GPS devices, and thus are not strictly comparable. The spatial position of each group was recorded with a Garmin GPS from the moment the tamarins left their sleeping site (at around 05:30) until the moment they arrived at their next sleeping site (at around 16:00) (Culot et al., 2011; Lledo-Ferrer et al., 2011). During the day,

the group's position was recorded at varying time intervals, according to the movement of the group.

The saddle-back tamarin data were originally collected for behavioral studies. In 2004, the focus was on vocal communication and coordination of group movements (unpublished), in 2007 and 2008 on territoriality and scent marking (Lledo-Ferrer et al., 2011), in 2009 on variability in feeding ecology (Kubisch, 2009), and in 2011 on the effects of forest successional status on foraging (Kupsch et al., 2014).

All three saddle-back tamarin groups lived in association and shared the home-range each with a group of mustached tamarins. Over a 10-year period (2004–2014), mean group size and variation in group size for each species and for both species combined were similar (Table S1).

2.3 | Fern and lycophyte inventory and soil sampling

We carried out a floristic inventory at EBQB in 2010. We recorded the abundance of fern and lycophyte species along 11 line transects. These lines followed the east-west oriented permanent primate observation trails but we established them 15 m south of the nearest trail in order to avoid the disturbance effect of the trail. All transects were 5 m wide, but their length varied between 500 m and 1475 m. We divided the transects into 25-m subunits. Along the transects, we recorded every individual with at least one green leaf (leafy stem in the case of lycophytes) ≥ 10 cm in length. We also included epiphytes and hemiepiphytes if they had leaves within 2 m of the ground surface. We collected a representative specimen of every species and morphospecies found, and additional specimens of individuals that we could not refer with certainty to an already collected species or morphospecies. We pressed the specimens between

newspaper sheets, preserved with alcohol and stored in plastic bags until they could be transported to Iquitos and dried at the Herbarium Amazonense (AMAZ; acronyms according to Thiers, continuously updated). We deposited the first set of vouchers at AMAZ and the duplicates at the University of Turku Herbarium (TUR), Finland.

We collected twenty soil samples at various points along the plant survey transects. One or two samples were taken along the short transects and up to three from the long ones to cover the entire trail network. Of these, we took 12 well within the limits of a 25 m transect subunit, and the remaining 8 at the limit between two subunits. We collected the soil samples from the top 5 cm of the mineral soil (after removing the organic layer). Each sample was composed of 5 subsamples gathered within a circular area 5 m in diameter. We dried the samples at room temperature and stored them in plastic bags until they were analyzed at MTT Agrifood Research Finland for the concentration of exchangeable base cations (Ca, Mg, K). Spatial variation in exchangeable bases has previously been found to explain patterns in plant species composition at various spatial extents in Amazonia (Higgins et al., 2011; Poulsen et al., 2006; Ruokolainen et al., 2007; Suominen et al., 2013; Tuomisto et al., 2016; Tuomisto, Poulsen, et al., 2003; Tuomisto, Ruokolainen, Aguilar, et al., 2003; Zuquim et al., 2014).

2.4 | Floristic and soil reference data

In order to place EBQB within a broader floristic and environmental context, we compared our data on fern and lycophyte species composition and soil cation concentration to data collected with the same sampling methods from 227 reference transects located across western Amazonia. These reference transects were 5 m wide and 500 m long, and all of them represented non-inundated forest. Three soil samples were available from each reference transect, and we used the one with the median base cation concentration value for that transect. The corresponding floristic data were extracted from a 100-m section of the transect centered on the selected soil sample. The transects have been described in detail in Tuomisto, Poulsen, et al. (2003), Tuomisto, Ruokolainen, and Yli-Halla (2003), Tuomisto et al. (2016) and Higgins et al. (2011). Out of the total set of transects in the earlier studies, we excluded those in the Department of Madre de Dios, because they have a drier climate than our study area (Senamhi, 2020), and those along the Pastaza river and the nearby oil road, because their soil samples were pooled across the entire transect before laboratory analysis and could not be referenced to a specific 100-m section. We used the remaining data to generate a model of the relationship between floristic composition and soil base cation concentration across western Amazonia. Subsequently, we used this model to infer soil base cation concentration at EBQB.

2.5 | Estimating tamarin home-range size

We estimated the home-range size (HRS) and position of each of the three tamarin groups based on the georeferenced data. We converted

the coordinates of the monkey observations into a spatial points data frame using the package *sp* v. 1.3-2 (Pebesma et al., 2018) in the R language (R Development Core Team, 2019). Then, we calculated home-range polygons from the coordinates using the 95% kernel utilization distribution (assuming a bivariate normal kernel) with the function *kernelUD* in the R package *adehabitatHR* v. 0.4.16 (Calenge, 2006). We used data from individual years to examine how much the estimated range size and position varied from year to year for each tamarin group (five years' data for G1 and G3, three years' data for G2).

Georeferenced data from 3 years (2004, 2007 and 2008) were available for all three tamarin groups. We pooled these to calculate a final 95% kernel utilization distribution polygon for each tamarin group. We used these polygons as input data when estimating soil conditions for the forest occupied by each tamarin group.

2.6 | Estimating soil characteristics

We calculated fern and lycophyte species density for each home-range separately as the average number of species encountered in those 100-m transect subunits that fell within each home-range polygon.

To map soil base cation concentration at EBQB, we used the weighted averaging approach (ter Braak & van Dam, 1989). This involved first calculating soil base cation concentration optima for the observed fern and lycophyte species on the basis of the western Amazonian reference dataset, and then using these optima to predict base cation concentration in the EBQB sampling units on the basis of their fern and lycophyte species composition. A species' optimum value for an environmental variable is defined as the average environmental variable value at the sites where the species has been observed (ter Braak & van Dam, 1989). We calculated the log-transformed base cation optimum of each species by averaging the log-transformed soil base cation concentration values ($\log_{10}[\text{Ca} + \text{Mg} + \text{K}]$) from those plots in which the species had been encountered, corrected for uneven environmental sampling following Jones et al. (2016). Then, we obtained the estimates of local soil base cation concentration by calculating the average of the log-transformed base cation optima of the species that were present in the sampling unit of interest and back-transforming the value to a linear scale by the exponential function.

Because predictions are based on averaging optima, which are themselves averages, low values tend to be overestimated and high values underestimated, which leads to the predictions having a smaller range than the original observations. Therefore, we applied inverse linear deshrinking following Suominen et al. (2013) to expand the range of the soil cation predictions to the originally measured length of the cation concentration gradient. The correlation between measured (based on soil samples) and predicted soil cation concentrations in the 227 transects comprising the Western Amazonian reference dataset was very high ($R = 0.93$, $p < 0.0001$), indicating that our method provided robust estimates of cation concentration across the region.

We then predicted soil cation concentrations within each subunit of EBQB transects. These predictions were made at two spatial resolutions: (a) original subunits of 5 m × 25 m and (b) subunits of 5 m × 100 m obtained by combining four consecutive 25-m subunits. Because a 25-m subunit does not fall precisely in the center of a 100-m transect section, predictions at the 100-m resolution were first made for two 100-m-sections, one with the midpoint just before the focal 25-m subunit and one with the midpoint just after, and the average of these two predictions was used in the analyses.

We assessed the accuracy of the soil cation concentration predictions within EBQB by calculating the correlation between the predicted and measured values for the 20 subunits with soil samples. We also correlated the predicted base cation concentrations with subunit elevation extracted from a 30-m resolution SRTM digital elevation model using the raster package v. 3.0-7 (Hijmans et al., 2019) in R (R Development Core Team, 2019). This was done because soil properties often vary systematically along local topographic gradients.

Finally, we used the base cation concentration predictions obtained with the spatial resolution (25-m or 100-m) that performed best to calculate the average predicted soil base cation concentration within the home-ranges of each of the three tamarin groups.

3 | RESULTS

3.1 | Floristic and soil characteristics of Estación Biológica Quebrada Blanco in a Western Amazonian context

We found 81 species of ferns and lycophytes in the 12 km of transects (6 ha) inventoried at EBQB. Most of these species were typical of soils with low or very low base cation concentration in a western Amazonian context (e.g., *Adiantum tomentosum* Klotzsch, *Selaginella parkeri* (Hook. & Grev.) Spring, *Asplenium hallii* Hook., *Lindsaea falcata* Dryand., *Trichomanes bicornne* Hook.) (Ruokolainen & Tuomisto, 1998; Tuomisto & Poulsen, 1996; Tuomisto, Ruokolainen, Aguilar, et al., 2003; Zuquim et al., 2014). Only the topographically lower-lying SW and NW corners of the study area had some fern species typical of moderately cation-rich to cation-rich soils, such as *Mickelia nicotianifolia* (Sw.) R.C. Moran, Labiak & Sundue, *Mickelia guianensis* (Aubl.) R.C. Moran, Sundue & Labiak, and *Campyloneurum fuscocquamatum* Lellinger.

Cation optima calculation was done for only 61 of these species, because 20 species were not present in the western Amazonian reference dataset. The estimates of soil base cation concentration obtained using fern and lycophyte species optima were mostly at the low end of the soil cation concentration gradient covered by the western Amazonian reference dataset (Figure 2). The estimates were also relatively uniform, except that a small low-elevation area in the south-western part of the study area (closest to the Quebrada Blanco river) was estimated to have more cation-rich soils. At the 25-m resolution, predicted soil

cation concentration in the EBQB fern transect subunits averaged 0.13 cmol(+)kg⁻¹ (range 0.03–4.74). At the 100-m resolution, the average was practically the same (0.14 cmol(+)kg⁻¹) but the predicted range was smaller (0.05–1.87).

These species-based inferences about the soils were supported by the results from the twenty soil samples: measured soil base cation concentrations averaged 0.18 cmol(+)kg⁻¹ and their range was 0.07–0.38 cmol(+)kg⁻¹ (Figure 2). From these values, it appears that our soil samples did not cover the high end of the soil cation concentration gradient at EBQB. Indeed, the estimated and measured ranges in soil cation concentrations were more similar within the set of transect subunits that was actually sampled for soils (estimated range 0.03–0.85 cmol(+)kg⁻¹ at the 25-m resolution and 0.05–0.50 cmol(+)kg⁻¹ at the 100-m resolution).

The correlation between predicted soil base cation concentrations generated at the 25-m and 100-m spatial resolutions was high ($R = 0.86$). Nevertheless, subunit altitude was slightly better correlated with the predictions made at the 100-m resolution than at the 25-m resolution ($R = -0.63$ vs. $R = -0.56$). Negative correlations reflect the fact that cation-rich soils tended to be found at lower topographic positions and cation-poorer soils at higher topographic positions.

The edaphic gradient sampled at EBQB was rather short, as all base cation concentrations were relatively similar when compared to the Western Amazonian reference data set (Figure 2). Nevertheless, the correlations between the predicted and measured soil cation concentration values were moderate for those 12 soil samples that were georeferenced to a single transect subunit ($R = 0.64$ for the 100-m resolution predictions and $R = 0.63$ for the 25-m resolution predictions; sites indicated by dark blue circles in Figure 2). When we included those 8 soil samples that were less accurately georeferenced (to a 50-m transect section; sites indicated by light blue circles in Figure 2), the correlations between measured and predicted values were much lower, especially due to one outlier value ($R = 0.16$ at the 100-m resolution, and $R = 0.15$ at the 25-m resolution).

3.2 | Soil base cation concentration within tamarin group home-ranges

The estimated home-ranges of the three tamarin groups had relatively constant core positions from year to year (Figure 3). However, their estimated HRSs varied between years by up to 48% (for tamarin group G3).

There was no consistent temporal pattern in the relative HRSs of the three tamarin groups. During those 5 years in which the tamarin groups were observed, groups G1 and G2 had their largest home-ranges in 2008, but group G3 had its largest home-range in 2004 (Table 1). During those 3 years for which data for all three tamarin groups were available (2004, 2007, and 2008), the annual estimated HRS for tamarin G2 was always larger than that for tamarin groups G1 and G3, whereas those of tamarin groups G1 and G3 were more similar (Table 1). The annual values ranged from 67–81 ha for G2, 33–49 ha for G3, and 32–41 ha for G1. When we combined data

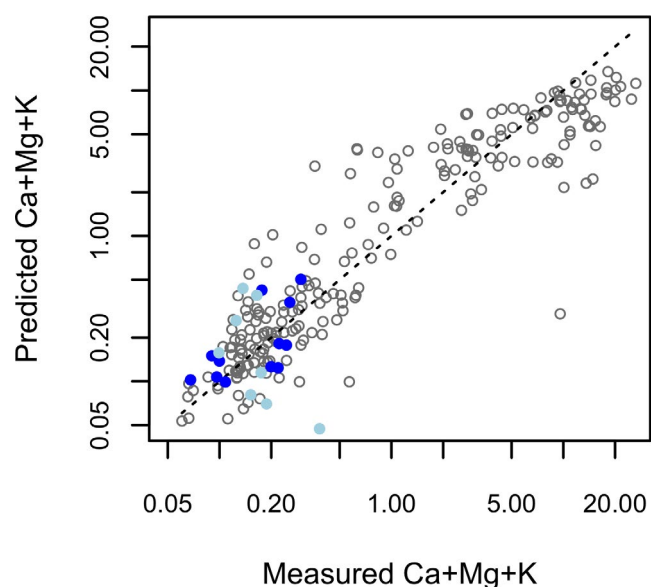


FIGURE 2 Predicted vs. measured soil base cation concentration ($\text{cmol}(+)\text{kg}^{-1}$ dry soil) in 227 transects, each $5\text{ m} \times 100\text{ m}$ in area, in lowland western Amazonia (black open circles), and for 20 soil sample sites within fern transects of varying length at the Estación Biológica Quebrada Blanco (EBQB) in Peru (blue circles). At EBQB, 12 soil samples were georeferenced to a single $5\text{-m} \times 25\text{-m}$ subunit of the fern transects (dark blue circles), whereas 8 soil samples were less precisely georeferenced to a 50-m transect section (light blue circles). Cation sum predictions in each case are based on the average calculated soil optima of fern and lycophyte species encountered in either the entire transect (western Amazonia) or in a 100-m transect section centered on the subunit(s) in which soil samples were collected (EBQB). The correlation between measured and predicted values in the western Amazonian dataset = 0.93, that for the precisely georeferenced soil samples at EBQB = 0.64 and for all EBQB soil samples = 0.16. The diagonal represents the line of perfect prediction

from these 3 years of observation to generate a final 95% kernel home-range estimate for each group, the corresponding values were 76 ha for G2, 40 ha for G3, and 39 ha for G1 (Table 1, Figure 3).

At the 100-m resolution, predicted soil base cation concentrations were found to differ between the home-ranges of the tamarin groups (95% kernels calculated from 3 years of data). The highest base cation concentration was predicted for the home-range of G1 ($0.28 \pm 0.31\text{ cmol}(+)\text{kg}^{-1}$), and the predictions for G3 ($0.16 \pm 0.08\text{ cmol}(+)\text{kg}^{-1}$) and G2 ($0.13 \pm 0.06\text{ cmol}(+)\text{kg}^{-1}$) were clearly lower (Figure 4).

4 | DISCUSSION

4.1 | Habitat characteristics of EBQB in a western Amazonian context

Our data clearly demonstrate that the soils at EBQB have relatively low base cation concentrations and are representative of the nutrient-poor end of the western Amazonian soil spectrum. This

was directly supported by the chemical analyses of the twenty soil samples collected at EBQB and also by our cation concentration estimates based on fern and lycophyte species optima. Indeed, most of the fern and lycophyte species that we found at EBQB are associated with poor to intermediately poor soils elsewhere in Amazonia (Cárdenas et al., 2007; Salovaara et al., 2004; Tuomisto et al., 2016; Tuomisto & Poulsen, 1996; Zuquim et al., 2014). Therefore, we conclude that the EBQB forests have relatively low primary productivity and, consequently, low carrying capacity for herbivores.

Overall, both floristic composition and soil properties at EBQB closely resemble those on soils derived from the Nauta Formation of Late Miocene to Pliocene age and on river terraces (Higgins et al., 2011; Salovaara et al., 2004; Tuomisto et al., 2016). This is a widespread habitat type in western Amazonia (Tuomisto et al., 2016, 2019) that is also common in the Allpahuayo-Mishana National Reserve, another area in northern Peru with a history of intensive primate studies. In contrast, the floristic compositions around Cocha Cashu biological station in southern Peru and the Yasuni National Park in Ecuador are very different and the soils have several times higher base cation concentrations (Tuomisto, Ruokolainen, & Yli-Halla, 2003; Tuomisto et al., 2019), and by inference also higher primary productivities and higher carrying capacities. Taking such habitat differences into account can provide new insights into the factors responsible for differences in ecological results across studies carried out at different sites.

Fern and lycophyte species composition across EBQB was relatively uniform. However, those fern and lycophyte species that are associated with extremely poor soils, such as white sands (e.g., *Trichomanes bicorne*), elsewhere in western Amazonia were mostly found in the center of the EBQB study area. In contrast, species associated with more cation-rich soils in other areas (e.g., *Mickelia nicotianifolia*, *Mickelia guianensis*) were only found in the NW and SW corners of the EBQB study area (Figure 4). Fern and lycophyte species richness has in general been found to increase with soil cation concentration in Amazonia (Tuomisto et al., 2014), and this was also the case at the local scale at EBQB: within-subunit species density was highest in the SW corner of the study area where the soil cation concentrations were highest.

EBQB is very close to the border between an old terrace of the Amazon river and the Pebas Formation (Figure 1; Kalliola et al., 1998). The Pebas Formation has, in general, heavy clay soils with high base cation concentrations, and it is possible that the low-lying corners of our study area have had some cation inputs from the Pebas Formation. Alternatively, more cation-rich sediments may have been deposited by the white-water Quebrada Blanco river during its annual floods. With this exception, our results indicate that the entire study area is firmly on the terrace side of the geological boundary, and that the results of ecological studies undertaken at this site may be most directly comparable with those undertaken at other relatively poor-soil sites in Western Amazonia.

4.2 | Saddle-back tamarin home-range size

The HRSs of saddle-back tamarin groups at EBQB varied somewhat between years. In broad terms, our results based on 3 years of

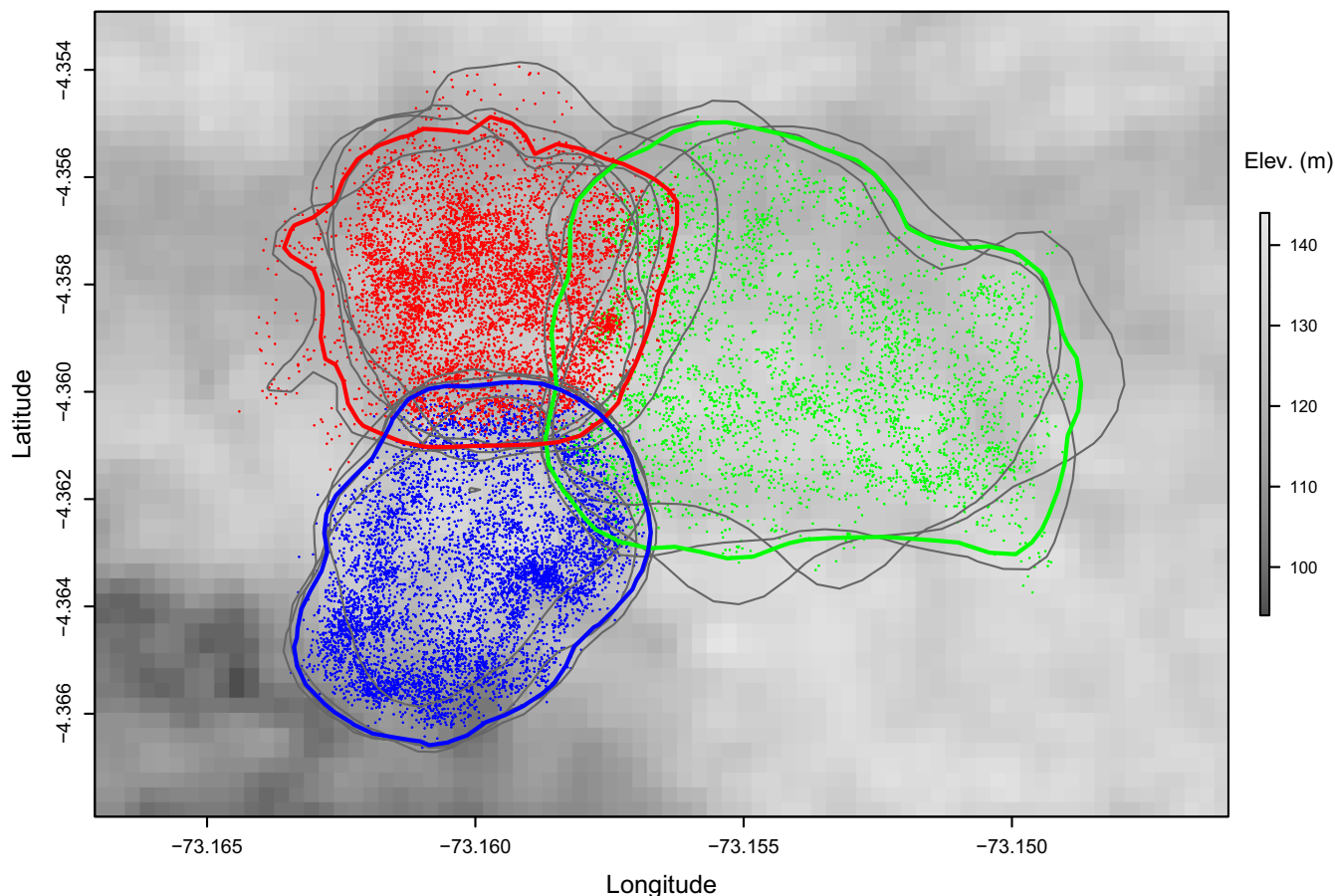


FIGURE 3 Saddle-back tamarin observations (points) and calculated 95% kernel utilization distributions (polygons) of three tamarin groups (G1—blue, G2—green, G3—red) at the Estación Biológica Quebrada Blanco, Peru, superimposed on a greyscale 30-m resolution Shuttle Radar Topography Mission (SRTM) model of altitude (m a.s.l.). home-range kernels were calculated on the basis of three (G2) or five (G1, G3) years of observations recorded between 2004 and 2011 ($n = 16,195$ georeferenced points in total). Annual kernels for each tamarin group are illustrated with narrow black lines. Final kernels, combining those 3 years during which all three tamarin groups were tracked (2004, 2007 and 2008), are illustrated with thicker lines in the same color as the point observations corresponding to that tamarin group

TABLE 1 Saddle-back tamarin home-range areas (ha) for each of three groups (G1, G2, and G3) at the Estación Biológica Quebrada Blanco, Peru

| Year(s) | G1 | G2 | G3 |
|------------------|----|----|----|
| 2004 | 32 | 67 | 49 |
| 2007 | 40 | 78 | 38 |
| 2008 | 41 | 81 | 35 |
| 2009 | 33 | – | 35 |
| 2011 | 35 | – | 33 |
| 2004, 2007, 2008 | 39 | 76 | 40 |

Note: home-ranges were estimated in five individual years (three individual years for G2) and then based on 3 years' combined observations (lowest row). home-ranges were defined as the 95% kernel utilization distribution.

observations (2004, 2007, and 2008) were consistent with the findings of Lledo-Ferrer et al. (2011) based on the years 2007 and 2008 only: G2 had a much larger home-range than G1 and G3. Lledo-Ferrer et al. (2011) suggested that G1 inhabits a slightly smaller area

than G3, but a later study based only on data from the year 2011 (Kupsch et al., 2014) found a similar HRS for both monkey groups. Since mean group size and the range of group size are very similar between the three groups (and also for the associated mustached tamarins and for both species combined; Table S1), HRS variation cannot be explained by variation in tamarin group size.

In our data, the estimated HRSs of G1 and G3 were very similar. However, it should be noted that G3 has in recent years sometimes been observed to cross Quebrada Choroy, which is at the northern limit of the study area and of the observed G3 home-range. The periods of time involved have been short, but since the group could not be followed across the stream, the characteristics of these visits have not been quantified (Heymann pers. obs.). Therefore, our estimates of the home-range of G3 are underestimated to an unknown degree. It is possible that the inclusion of these occasionally visited areas would have increased the home-range of G3 beyond that of G1. Based on the available data, it nonetheless seems clear that G2 is the widest ranging of the three groups, as our estimate for the HRS of G2 was almost twice those of G1 and G3.

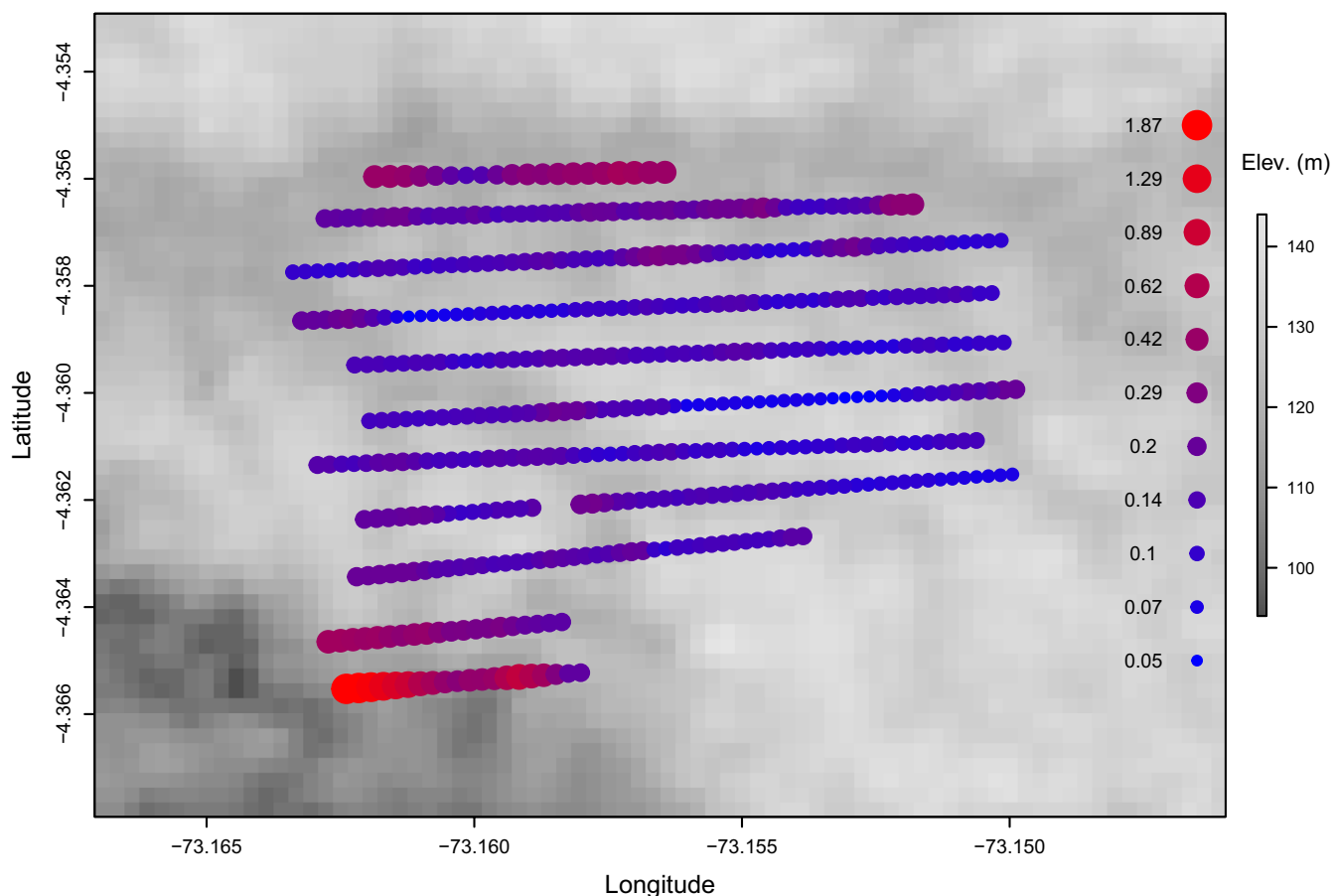


FIGURE 4 Predicted soil base cation concentration ($\text{Ca} + \text{Mg} + \text{K}$ in $\text{cmol}(+)\text{kg}^{-1}$ of dry soil) in fern transect subunits (each $5 \text{ m} \times 25 \text{ m}$) at the Estación Biológica Quebrada Blanco (EBQB), Peru. Circle size and color indicate predicted soil cation concentration, with large red circles indicating the richest soils and small blue circles indicating the poorest soils. Predictions are based on soil cation concentration optima of the fern and lycophyte species that were encountered in a 100-m transect section centered on each subunit. Soil predictions are superimposed on a greyscale 30-m resolution SRTM map of altitude (m a.s.l.)

4.3 | Linking inferred soil fertility with home-range size (HRS)

By linking the substantial existing tamarin monitoring data at EBQB with our predicted soil data, we demonstrate the potential of this approach for future testing of hypotheses linked to the bottom-up control of animal population structure, dynamics, and behavior. Our results, although limited to three tamarin groups at present, also provide a point of comparison for future studies. If tamarin HRS is determined by food (fruit) availability (Janzen, 1974; Kricher, 2011), our expectation is that it will also correlate with soil nutrients, because these influence numerous relevant properties of the vegetation (e.g., species composition, primary productivity, and plant palatability). We observed that the saddle-back tamarin group at EBQB with the largest home-range (G2) indeed occurred in an area with more nutrient-poor soils than the other two groups, and the group with the smallest home-range (G1) occurred in an area with somewhat more fertile soils. However, the home-range of the third group (G3) was almost as small as that of G1, although the soils were estimated to be almost as nutrient-poor as those of G2. There may

be numerous biological explanations for this result. It may be that soil variation within EBQB is in fact too limited to have a consistent effect on primate HRS. Alternatively, it is possible that the home-range of G3 contained some particularly productive fruit trees, compensating for the lower average productivity expected in poor soils. It is also possible that the results reflect sampling limitations. As described above, the home-range of G3 extended beyond the area of intensive survey, and its size was therefore underestimated to an unknown degree.

A robust test of the hypothesis that site productivity affects HRS would be to replicate this approach over multiple primate groups across a greater variety of soil formations. For example, if bottom-up control of carrying capacity is an important factor determining tamarin HRS, we would expect HRSs to be smaller 10 km east of EBQB than they are at EBQB itself. This is because further east the soils are derived from the more cation-rich Pebas formation, which is also reflected in the local fern flora (Kalliolla et al., 1998; Suominen et al., 2015). Therefore, in that area we would expect higher primary productivity, a higher density of fruit, and less need for primates to forage widely (Janzen, 1974). Because primate

inventories are very laborious, whereas fern and lycophyte inventories are relatively quick, a faster way to test the relationship between size and quality of primate home-ranges would be to return to sites where intensive primate studies have already been done, and to inventory ferns and lycophytes there. We suggest that this would help to shed new light on primate ecology in a simple and cost-efficient way.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in EUDAT at <https://doi.org/10.23728/b2share.3ab75222a3ff4fb ebe922db6cdfc980b>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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